

A RECONSIDERATION OF *BRODIAEA MINOR* (BENTH.) S. WATSON AND
BRODIAEA PURDYI EASTWOOD (THEMIDACEAE), WITH THE
RESURRECTION OF *BRODIAEA NANA* HOOVER

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ABSTRACT

A review of taxonomic literature, examination of existing herbarium specimens, and a morphological study of field-collected material demonstrates that species circumscriptions have been misapplied for the small-flowered *Brodiaea* species with spreading perianth lobes and floral tubes narrowed above the ovary. The results of these studies demonstrate that Niehaus's (1971) concept of *B. purdyi*, polyploid plants that occur in woodland habitats in the northern Sierra Nevada foothills, applies to the taxon originally described as *B. minor*, placing *B. purdyi* in synonymy with *B. minor*. Niehaus's concept of *B. minor*, diploid plants occurring in vernal pool terrain, applies only to those populations originally described as *Brodiaea nana*, which is resurrected at species rank.

Key Words: Themidaceae, *Brodiaea*, taxonomic revision, California.

The genus *Brodiaea* (Themidaceae) consists of approximately 14 or 15 species, almost entirely restricted to the California Floristic Province (Niehaus 1971, 1980; Keator 1993; Pires 2002). *Brodiaea* has a rich taxonomic history and has been placed variously in Liliaceae, Amaryllidaceae, and Alliaceae (Hoover 1939; Keator 1967, 1989; Niehaus 1971, 1980). Recent phylogenetic studies, however, place *Brodiaea* and relatives not with *Allium* but with Hyacinthaceae and other families (Fay and Chase 1996; Fay et al. 2000; Pires et al. 2001; Pires and Sytsma 2002). As a result, *Brodiaea* has been reassigned to the family Themidaceae or a more inclusive Asparagaceae (Angiosperm Phylogeny Group 2003).

These studies have focused on relationships among families and genera and have not addressed relationships within *Brodiaea*, which remain poorly resolved despite having been monographed twice (Hoover 1939; Niehaus 1971). Species circumscriptions and relationships among species historically have been difficult to elucidate, largely because study of fresh material is crucial for comparison of the diagnostic floral features, which are obliterated when specimens are pressed and dried (Greene 1886; Hoover 1939). Pires (2002) points out the need to prepare open flowers when making herbarium specimens, but even with fresh material, making a determination with confidence can often be frustrating.

The small-statured species with spreading perianth lobes and floral tubes that are narrowed above the ovary exemplify this taxonomic difficulty. Current floristic treatments of *Brodiaea* (Keator 1993; Pires 2002) recognize two species, *Brodiaea minor* (Benth.) S. Watson and *Brodiaea purdyi* Eastwood, based on Niehaus's (1971) monograph of the genus. Niehaus differentiated

between the two species based on morphology, cytology, and ecology. However, it is often not possible to assign specimens unambiguously to one or the other species, using the current taxonomic keys (Oswald 1994; personal observation).

In this paper, I show that the frustration with species determinations using current floristic treatments is not due simply to an inadequate diagnostic key, but stems from a more fundamental error. I provide a morphometric analysis supporting Niehaus's recognition of two taxa at species rank, but I demonstrate that Niehaus misapplied the name *B. minor* and did not correctly circumscribe all populations under the correct species concepts. I discuss the source of Niehaus's error and clarify the nomenclature. In addition, I discuss the relationship of these two species with other members of the genus.

METHODS

I examined herbarium specimens of *B. minor* and *B. purdyi*, as circumscribed by Niehaus (1971), in the principal collections of both species (herbaria consulted: JEPS, UC, CHSC, DAV) and photographs of the types of *B. minor*, *B. purdyi*, and *B. nana*. I sampled 36 populations throughout the ranges, based on localities provided on the specimen labels. I collected fresh material and dissected one flower from 10 plants in each population, using flowers at approximately the same stage of anthesis, to minimize variation due to any change in flower size from the beginning to the end of anthesis. I measured 11 floral characters and noted the shape and position of the floral parts. I employed principal components analysis, using the SYSTAT 11

statistics package (SYSTAT Software, Richmond, CA), to reduce the number of variables and simplify the morphological comparison. The analysis was performed using the mean floral measurements from each population. Factor scores for the first two principal components were then plotted to determine whether discrete groups of populations could be recognized.

RESULTS AND DISCUSSION

Taxonomic Review

Theodor Hartweg collected the type of *Brodiaea minor*. In the spring of 1847, he had traveled to California on a mission to collect botanical specimens for the Horticultural Society of London (Hartweg 1848). Hartweg made numerous collections during his stay at the ranch of "Mr. L.", in the northern Sacramento Valley (undoubtedly Peter Lassen, who homesteaded in southern Tehama County, near the present town of Vina (Swartzlow 1964)). During a visit to the foothills east of the ranch, he collected specimens that later became the type of *Brodiaea grandiflora* Sm. var. *minor* Benth. Sereno Watson (1879) later raised var. *minor* to species rank.

Greene (1894) apparently initiated some confusion by applying the name *B. minor* to all of the small-flowered brodiaeas in the Central Valley and adjacent Sierra Nevada foothills. Subsequently, Alice Eastwood (1896) described a "new" species from the northern Sierra Nevada foothills, *Brodiaea purdyi*, noting the long, narrow perianth lobes as the distinguishing feature of this species. Jepson (1922) recognized that Greene had encompassed several different taxa under the name *B. minor* and that *B. purdyi* was synonymous with *B. minor*, as originally described by Bentham. Jepson applied the name *Brodiaea synandra* (Heller) Jepson to the small-flowered plants of the Central Valley that, like *B. minor*, had the perianth tube narrowed above the ovary. Unfortunately, Jepson did not have access to the type specimen of *B. synandra*, which actually is conspecific with the earlier-published *Brodiaea leptandra* (E. Greene) Baker. Jepson also repeated Greene's error, citing specimens now assigned to several different species, including *B. coronaria* and *B. terrestris*, within his circumscription of *B. synandra*.

Hoover (1936, 1939) eventually sorted out the nomenclatural confusion. Hoover (1939) was the first to monograph the genus and developed most of the species concepts that are still used to circumscribe the taxa. *Brodiaea* species have traditionally been differentiated on the basis of the shape and position of the floral parts, and Hoover followed this tradition by recognizing species when there were discrete differences in morphology and recognizing varieties when taxa

differed primarily in the size of the floral parts. For the small-flowered plants along the east side of the Central Valley, he proposed the name *Brodiaea nana*, because of their small stature, having scapes less than 5 cm tall. Hoover (1939) subsequently reduced *B. nana* to a variety of *B. minor*, citing his observations that the two taxa intergraded morphologically.

Niehaus (1971) expanded on Hoover's work with *Brodiaea* by incorporating observations from anatomy, cytology, palynology, flavonoid chemistry, ecology, and hybridization studies. Although his study tended to support Hoover's taxonomic framework, he expanded some of the morphologically-based species concepts in *Brodiaea* to include data from cytology and ecology. Niehaus recognized two small-statured, small-flowered species with spreading perianth lobes and floral tubes that are narrowed above the ovary, one consisting of populations of diploid ($n = 6$) plants growing in vernal pool terrain along the eastern edge of the Central Valley, the other consisting of tetraploid ($n = 12$) and octaploid ($n = 24$) populations occurring in foothill habitats, often on gabbro or serpentine. To the former species, which essentially followed Hoover's concept of *B. nana*, he applied the name *B. minor*, placing *B. nana* in synonymy. He resurrected the name *B. purdyi* to apply to the latter species. Recent floristic treatments of *Brodiaea* (Keator 1993; Pires 2002) mostly followed Niehaus's treatment of the genus and maintained both *B. minor* and *B. purdyi* at species rank, although Keator noted that *B. purdyi* might merit placement as a subspecies of *B. minor*.

Morphological Study

The morphological study found that plants from the 36 sampled populations could be unambiguously assigned to one of two groups, but not to the groups represented by *B. minor* and *B. purdyi* as circumscribed by Niehaus (1971). First, two groups were differentiated by the shape and position of the stamens and staminodes. The first group of populations (Group A) had stamen morphology that was unusual for the genus and most similar to that described for *B. pallida* (Hoover 1938), including the presence of prominent papillae on the abaxial surface of the anthers (Fig. 1a). The connective broadened towards the apex, which was widely V-notched (Fig. 1a, b), and the filaments were short and abaxially winged (V- or Y-shaped in cross-section [Fig. 1c]). The staminodes were short, broad, and erect, with slightly inrolled margins (Fig. 1d, 2a). The styles were about 1.5 times longer than the ovary (Fig. 1e).

Stamen morphology in the second group of populations (Group B) was not remarkably different from that in many other *Brodiaea*

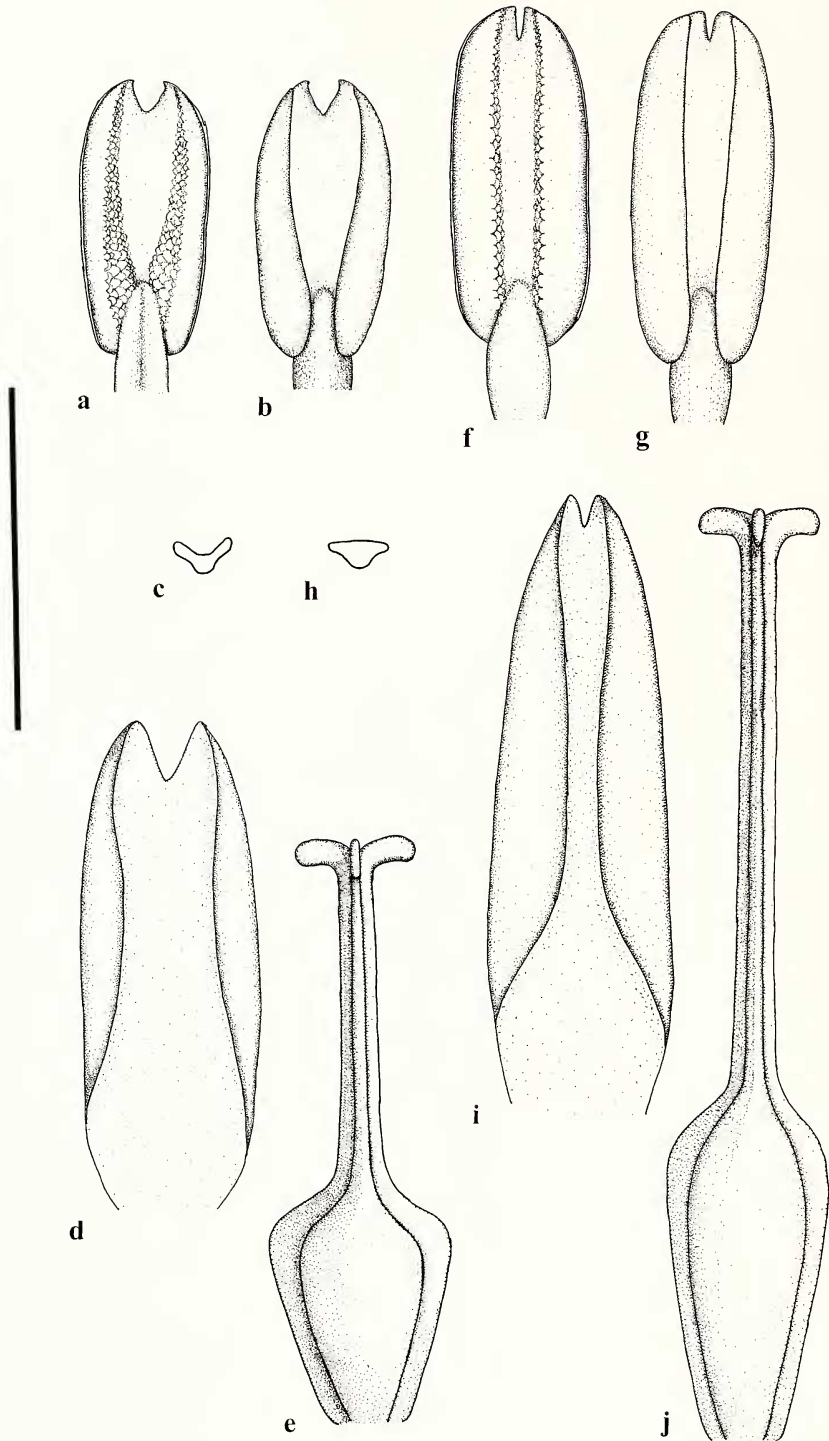


FIG. 1. Comparison of inner floral parts. A-E Group A (*Brodiaea nana* Hoover). F-J Group B (*Brodiaea minor* (Benth.) S. Watson). A, F. Stamen (adaxial view). B, G. Stamen (abaxial view). C, H. Filament (cross-section). D, I. Staminode. E, J. Pistil. The scale bar represents a length of 5 mm.

species. Abaxial papillae were present on the anthers but were not prominent (Fig. 1f). The connective was uniformly wide to only slightly broader at the apex, which was narrowly notched

(Fig. 1f, g), and the filaments were longer and laterally winged (T-shaped in cross-section [Fig. 1h]). The staminodes were longer and narrower with strongly inrolled margins (Fig. 1i)

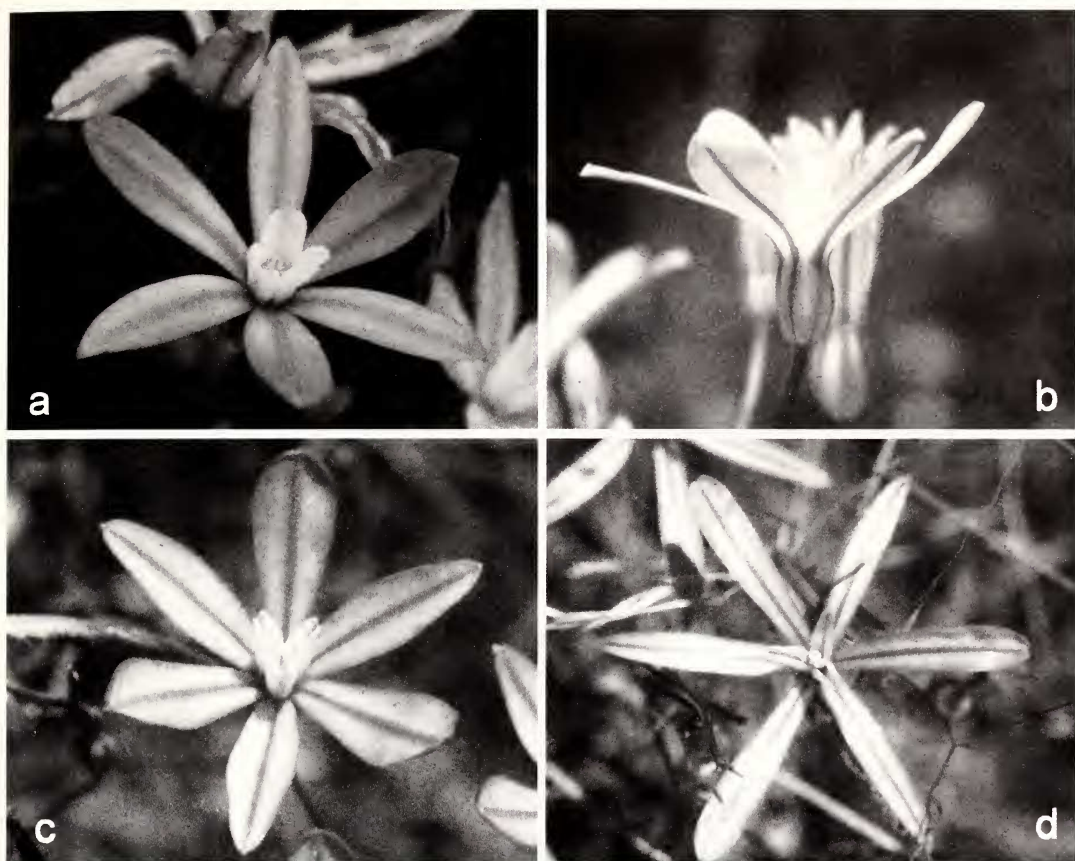


FIG. 2. Comparison of flowers. A, B *Brodiaea nana* Hoover. A. Top view. B. Lateral view, showing constriction above the ovary. C, D *Brodiaea minor* (Benth.) S. Watson. C. Typical form. D. Narrow-lobed form described as *B. purdyi* Eastw.

and were erect to recurved at the tip (Fig. 2c, d). The styles were about 1.75 times the length of the ovary (Fig. 1j).

The principal components analysis reduced the floral variables to two factors (Table 1). The first principal component, which explained almost 79% of the variation, appeared to be a size factor, primarily loading on length of the floral parts. The second principal component also appeared to be a size factor, but loading on the size of the perianth lobes (length and width). The plot of the two principal components also separated the populations into two groups that corresponded precisely with Groups A and B, but not to *B. minor* and *B. purdyi* as currently circumscribed (Fig. 3).

Group A corresponds closely to Hoover's (1936) original circumscription of *Brodiaea nana* and includes populations along the eastern edge of the Central Valley, ranging from Butte County to Merced County, where the type was collected. Group A includes all of the populations Niehaus (1971) determined to be diploid. Group B consists of populations Niehaus assigned to *B.*

purdyi but also includes populations he assigned to *B. minor*. Populations comprising Group B range from the Sierra Nevada foothills to the northern Sacramento Valley in Butte and Tehama Counties, encompassing the type localities of both *B. minor* and *B. purdyi*. Group B includes the populations Niehaus (1971) determined to be tetraploid and octaploid. Therefore, Group B corresponds to *B. minor* as circumscribed by Jepson (1922) and Hoover (1939), rather than Niehaus' (1971) later circumscription.

Brodiaea nana Resurrected

The results of the morphological analysis show that *B. nana* should be recognized as a taxon distinct from *B. minor*, and on both morphological and cytological grounds, *B. nana* warrants recognition at the rank of species. Hoover (1936) originally described *B. nana* at species rank, but he later (1939) reduced it to a variety of *B. minor*, citing his observation that specimens from Sacramento County were intermediate between *B. minor* and *B. nana*. Hoover did not elaborate

TABLE 1. RESULTS OF PRINCIPAL COMPONENTS ANALYSIS ON MEANS OF ELEVEN VARIABLES FROM SIXTEEN POPULATIONS OF *B. NANA* (GROUP A) AND 20 POPULATIONS OF *B. MINOR* (GROUP B).

Variable	PC 1	PC 2
Pedicle Length	-0.251	0.428
Perianth Tube Length	0.917	0.189
Perianth Lobe Length	0.531	0.529
Width, Inner Lobe	-0.411	0.859
Width, Outer Lobe	0.088	0.925
Staminode Length	0.958	0.071
Filament Length	0.924	0.127
Anther Length	0.930	-0.024
Ovary Length	0.951	-0.025
Style Length	0.983	0.011
Ovule Number	-0.758	0.299
Eigenvalue	6.446	2.204
Variation Explained	58.60%	20.04%

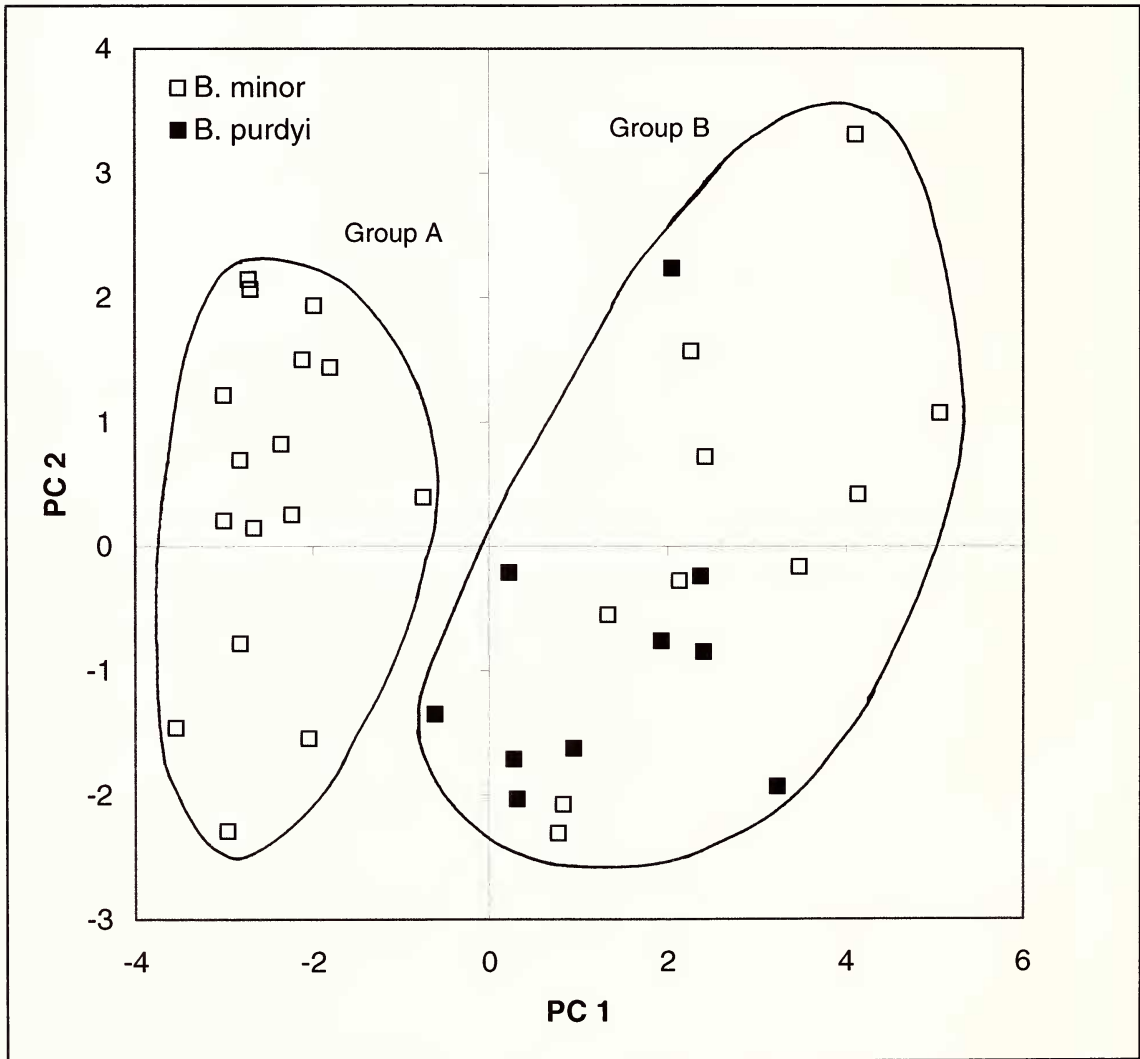


FIG. 3. Two-dimensional scatter diagram of first and second principal component scores based on population means of floral characters from *B. minor* and *B. purdyi* (*sensu* Niehaus [1971]). Group A corresponds to *B. nana* Hoover, and Group B corresponds to *B. minor* (*sensu* Jepson (1922) and Hoover (1939)).

TABLE 2. COMPARISON OF FLORAL CHARACTERS FOR *BRODIAEA MINOR* AND *BRODIAEA NANA*. Measurements were made on fresh material, from one flower per plant and 10 plants per population, from 20 populations of *B. minor* and 16 populations of *B. nana*. Measurements in mm.

Character	<i>Brodiaea minor</i>		<i>Brodiaea nana</i>	
	mean	range	mean	range
Pedicel	21.4	7-45	24.5	6-56
Perianth tube	8.6	6.5-11.5	7.3	5.0-9.0
Perianth lobes	15.0	9.8-20.5	14.3	10.0-21.0
Width, inner lobes	4.7	3.0-7.0	5.5	4.0-8.0
Width, outer lobes	3.7	2.8-5.0	3.8	3.0-5.0
Staminode	9.1	6.2-12.5	7.2	6.0-9.0
Filament	2.2	1.0-3.5	1.4	1.0-2.0
Anther	5.2	3.5-7.0	4.0	3.0-5.0
Ovary	4.9	3.2-7.0	3.5	2.5-5.0
Style	8.8	6.0-12.0	5.3	4.0-7.5
Ovule number	17.3	12-24	22.2	12-33

on which features were intermediate. The ranges for all floral part measurements do overlap, but on average, all floral parts of *B. nana* are smaller than those of *B. minor* (Table 2). It is more noteworthy that the shapes of the staminodes, stamens, and pistils consistently differentiate *B. nana* from *B. minor* (Fig. 1), because *Brodiaea* species traditionally have been recognized on the basis of the shape and position of the floral parts. Recognizing *B. nana* at species rank is also consistent with Niehaus's (1971) expanded species concepts in *Brodiaea*. Niehaus's (1971) diploid chromosome counts, a major criterion for re-establishing *B. nana* at species rank (albeit as *B. minor*), were all based on populations of *B. nana* as circumscribed by Hoover and confirmed as such by the present morphological study.

The distribution of *Brodiaea nana*, documented by herbarium specimens and confirmed by visits to the collection localities, ranges from Merced County north to Chico, in Butte County (Fig. 4). In addition, several disjunct populations of *B. nana* occur on volcanic mudflows adjacent to Payne's Creek and Battle Creek, in northern Tehama County and southern Shasta County. The distributions of *B. nana* and *B. minor* overlap in Butte and Tehama Counties, but the two species are almost never sympatric. However, I collected both species growing together at one location in Chico, Butte County. *Brodiaea nana* occurs in vernal swales, shallow vernal pools, and on the margins of deeper vernal pools.

Brodiaea minor Revisited and *Brodiaea purdyi* Reconsidered

It is clear that Niehaus's (1971) concept of *B. minor* applied only to those populations circumscribed by Hoover's *B. nana*. It is also clear that many of the populations Niehaus assigned to *B. minor* are morphologically indistinguishable from populations he assigned to *B. purdyi*. Niehaus's concept of two species, one consisting of diploid

populations occurring in vernal pool terrain, the other of polyploid populations occurring in foothill habitats, appears to have been only partially correct, as some populations of *B. minor* occur in vernal pool terrain. Moreover, he misapplied the names when circumscribing the populations that made up the two species. How did this error come about?

First, the flowers of both species are superficially similar (Fig. 2a, c), and many of the floral parts overlap in size (Table 2). Niehaus used scape length (=10 cm = *B. minor*, =10 cm = *B. purdyi*) and petal width (5-7 mm = *B. minor*, 4-5 mm = *B. purdyi*) as key characters for separating the two species. The type of *B. minor* (Hartweg 2002 [Isotype, NY]) has short scapes, and Niehaus evidently presumed that this population was assignable to the same taxon as Hoover's *B. nana*, and that the correct name for the taxon, therefore, was *B. minor*. However, the type locality of *B. minor* occurs in blue oak-foothill pine woodland (Hartweg 1848), not in vernal pool terrain. Moreover, scape length is not a reliable character for differentiating between *Brodiaea* taxa. Scape length varies both within and among *Brodiaea* populations and may be environmentally plastic, to some degree (Doalson 1999). The type specimen of *B. purdyi* (*Purdy s.n.* [CAS]), which illustrates this variation quite nicely, consists of three plants, one with a short scape, one with a long scape, and one with an intermediate-length scape. Petal width also overlaps between *B. minor* and *B. nana* (Table 2) and is not reliable for differentiating between them.

The results of this paper demonstrate that Niehaus's (1971) concept of *B. purdyi*, the polyploid small-flowered species, with spreading perianth lobes and floral tubes that are narrowed above the ovary, and that occurs in woodland habitats in the northern Sierra Nevada foothills, applies to the taxon originally described as *B. minor* and as recognized by Jepson (1922) and

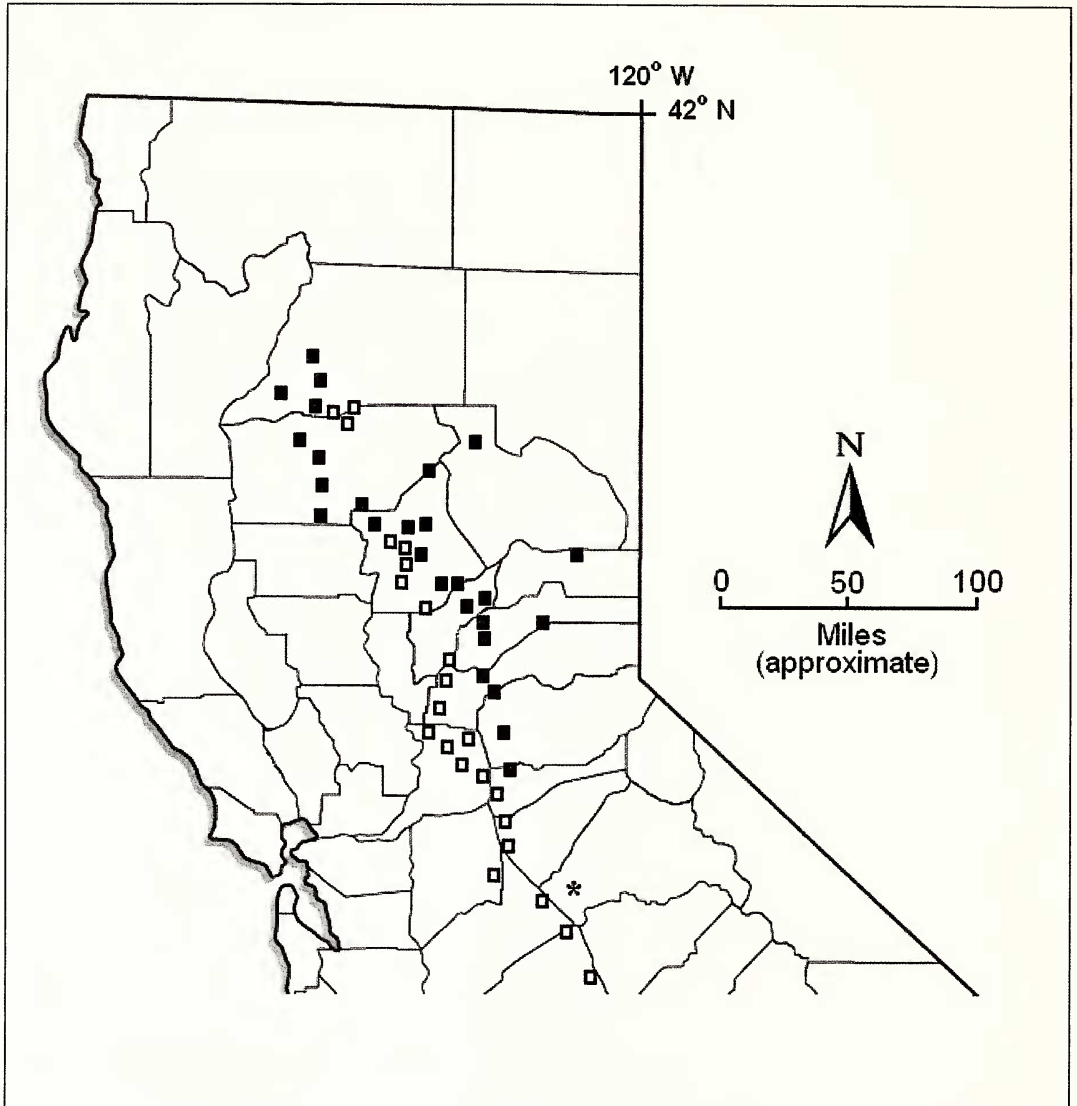


FIG. 4. Distribution of *Brodiaea minor* (■), *Brodiaea nana* (□), and *Brodiaea pallida* (*) in California, USA.

Hoover (1939), placing *B. purdyi* in synonymy with *B. minor*.

Currently, there is no basis for recognizing *B. purdyi* as a separate taxon. Eastwood (1896) noted that the original collections of *B. purdyi* were remarkable for their relatively long, narrow perianth lobes (Fig. 1d). In all other respects, however, including the shape and relative position of the floral parts, populations cannot be differentiated reliably. Moreover, there is substantial variation in perianth lobe length among populations of *B. minor*, and plants with long, narrow lobes appear to be at one end of a continuum of variation in lobe length (personal observation).

As recognized in this study and as documented by herbarium specimens, *Brodiaea minor* (in-

cluding *B. purdyi*) ranges along the eastern margin of the northern Sacramento Valley, from Shasta County to Butte County, into the Sierra Nevada foothills, and south to Amador County (Fig. 4). Most populations occur in vernal pool terrain, oak woodland, or chaparral, with a few populations occurring in dry montane meadows at higher elevations. Although some populations occur on gabbro or serpentine, *B. minor* does not appear to be restricted to those substrates.

Species Relationships

Relationships between *Brodiaea* species are poorly understood. Hoover (1939) recognized a series of infrageneric groups, based on floral morphology. He proposed four informal sections,

including section "Stellares", within which he placed *B. stellaris*, *B. pallida*, and *B. minor* (including *B. nana*). Niehaus (1971) added *B. insignis* to this group. Section "Stellares" is composed of small-flowered species with rotate corollas, broad staminodes, and short filaments that are more or less channeled on the abaxial side.

The strong morphological similarity between *B. minor* and *B. nana*, as shown in this study, supports a close relationship between these two species. Niehaus (1971) found that the flavonoid chemistry and floral vasculature of the two species was also very similar. *Brodiaea pallida* and *B. nana* appear to be closely related, as well. Both species are diploid ($n = 6$) and have similar flavonoid chemistry (Niehaus 1971), and their ranges overlap (Fig. 4). Their floral morphology is also quite similar. The perianth tube in *B. pallida* is not or only slightly narrowed above the ovary, but in both species the staminodes are erect and the margins only slightly inrolled. The anthers have prominent abaxial papillae, the connective broadens towards the apex (see Fig. 16 in Niehaus [1971]), and the filaments are abaxially winged, although the wings in *B. nana* are not as pronounced as in *B. pallida*. Hoover (1938, 1939) discussed at length the unusual morphology of the staminodes and stamens in *B. pallida*. His statement that these features were quite different from those of *B. minor* and his later treatment of *B. nana* as a variety of *B. minor* suggests that he was unaware of the similarities between *B. pallida* and *B. nana*.

Brodiaea stellaris and *B. insignis* appear to be less closely related to *B. nana*, *B. minor* and *B. pallida*. Flowers of *B. insignis* are at least superficially similar to those of *B. nana* and *B. minor* (unpublished data), although the floral tube is not constricted and the chromosome number ($n = 16$) and flavonoid compounds are substantially different than those two species (Niehaus 1971). In contrast, *B. stellaris* is a diploid ($n = 6$) with similar flavonoid chemistry to *B. nana*, *B. minor*, and *B. pallida*, but it is morphologically quite different from these species. Hoover (1939) originally grouped *B. pallida* with *B. stellaris* because the filaments of both species are prominently winged abaxially. In most other respects—shape of the perianth tube and lobes, staminodes, stamens, and ovary, and the relative proportion of these floral parts—*B. stellaris* is very different (unpublished data).

The following key to the species of section "Stellares" serves to differentiate between the species.

- 1a. Staminodes hooded at the tips, the margins not or only slightly incurving, connate at the base with the stamens; filaments with prom-

- inent apical appendages abaxially; North Coast Ranges, on serpentine *B. stellaris*
- 1b. Staminodes not hooded at the tips, the margins incurving to strongly inrolled, not connate at base with stamens; lateral margins of filaments winged, but appendages lacking.
- 2a. Perianth tube not narrowed above the ovary; filaments dilated at base; style shorter than ovary; southern Sierra Nevada foothills *B. insignis*
- 2b. Perianth tube narrowed above the ovary; filaments not or only slightly broader at base than at apex; style longer than the ovary.
- 3a. Staminodes erect to spreading, margins strongly inrolled; stamens narrowly notched at apex, lacking prominent papillae abaxially; filaments winged laterally, T-shaped in cross-section *B. minor*
- 3b. Staminodes erect, margins not to slightly inrolled; stamens broadly V-shaped at apex, with prominent abaxial papillae; filaments winged abaxially, V- or Y-shaped in cross section.
- 4a. Perianth lobes paler towards the base; perianth tube slightly narrowed above the ovary; staminodes as broad as or broader than the outer perianth lobes; central Sierra Nevada foothills, in swale, serpentine soil *B. pallida*
- 4b. Perianth color uniform; perianth tube strongly narrowed above the ovary; staminodes narrower than outer perianth lobes; eastern edge of Central Valley, in vernal pools and swales *B. nana*

Questions for Further Study

Although this study may have resolved the taxonomy of *B. minor* and *B. nana*, many phylogenetic questions remain. *Brodiaea minor* consists of populations of both tetraploids and octaploids. Niehaus (1971) postulated that *B. minor* was derived from diploid *B. nana*. Whether *B. minor* was derived via autopolyploidy or allopolyploidy is unclear. Whether octaploid *B. minor* was derived from *B. nana* or from tetraploid *B. minor* is also unclear. Moreover, the possibility exists that *B. minor* is a complex of polyploid populations of multiple origins, rather than a tetraploid lineage and an octaploid lineage.

The relationships between *B. pallida*, *B. minor*, and *B. nana* and other *Brodiaea* species remain uncertain. Reliance on morphological data alone has proved of limited usefulness in resolving relationships between and among *Brodiaea* species. Although groups of species can be recognized on the basis of unique characters, the phylogenetic relationships among the groups are still ambiguous. Niehaus (1971) provided some cytological, anatomical, and flavonoid data that may provide evidence for elucidating relationships, but little has been done to follow up on Niehaus's work. Niehaus's suggestion that eco-

logical data might be useful has also not been pursued.

Recent studies based on molecular data have proved useful for understanding relationships within the Themidaceae and may point a way towards resolving species relationships within *Brodiaea* (Pires and Sytsma 2002). Independent data sets derived from molecular data may help determine which morphological characters are plesiomorphic, which are derived, and which, like the "winged" filaments of *B. stellaris* and *B. pallida*, may be homoplastic. Molecular data may also be useful for differentiating between entities that have been derived via autopolyploidy or allopolyploidy (Rieseberg and Ellestrand 1993). *Brodiaea* remains a nearly untapped source for investigations on polyploidy, hybridization, and edaphic relationships.

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